

Infinite Series of Exact Equations in the Bak-Sneppen Model of Biological Evolution

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We derive an infinite series of exact equations for the Bak-Sneppen (BS) model in arbitrary dimensions. These equations relate different moments of temporal duration and spatial size of avalanches. We prove that the exponents of the BS model are the same above and below the critical point, and express the universal amplitude ratio of the avalanche spatial size in terms of the critical exponents. The equations uniquely determine the shape of the scaling function of the avalanche distribution. It is shown that in the BS model in arbitrary dimensions there is only one independent critical exponent. [S0031-9007(96)00781-8]

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Recently Bak and Sneppen [1] introduced a particularly simple toy model of biological evolution (the BS model). It provides a coarse-grained description of the behavior of the ecosystem of interacting species driven by mutation and natural selection. The features of the real evolutionary process, which may be correctly reproduced by this model, include the intermittent behavior (punctuated equilibrium), the apparent scale invariance of large extinction events [2], and the power law probability distribution of the lifetimes of species. In the simplest variant of the BS model the ecosystem consisting of L species is characterized by L numbers f_i arranged on a line. The number f_i represents the effective barrier for a successful mutation of i th species. At every time step the smallest number in the system is located, and this species is selected for mutation. As a result of this mutation this number, as well as two of its nearest neighbors (representing the species that strongly interact with a mutated one), are replaced with new uncorrelated random numbers drawn from the uniform distribution between 0 and 1. The generalization of these rules to higher spatial dimensions is straightforward. The BS model may describe the evolution on the longest time scale, where, due to universality, the exact microscopic details are of no importance.

In fact, there exists a whole class of models where the rules consist of selecting the site with the extremal (global maximal or minimal) value of some variable and then changing this variable and its nearest neighbors according to some stochastic rule. These models, referred to as *extremal models*, were extensively studied (for a recent review, see [3]). They were employed to describe a variety of physical phenomena such as fluid invasion in disordered porous media [4], low temperature creep [5], earthquake dynamics [6], etc. Among these models, the BS model occupies a special place similar to that of the Ising model in the equilibrium statistical mechanics, since many observations can be rigorously proven for the BS model and then applied to other extremal models based on numerical simulations and less rigorous arguments.

The feature of interest in the BS model (as well as in other extremal models) is its ability to organize itself into a scale-free stationary state. The dynamics in this critical state is given in terms of bursts of activity or *avalanches*, which form a hierarchical structure [1,3] of subavalanches within bigger avalanches. In the biological context these avalanches represent big extinction events. In this work we introduce a “master” equation for the avalanche hierarchy. It describes the cascade process in which smaller avalanches merge together to form bigger ones as the critical parameter is changed. From this equation we derive an *infinite series of exact* equations, relating different moments of temporal duration S and spatial area R^d of individual avalanches.

The master equation connects undercritical and overcritical regions of parameters. Given the existence of the scaling, we rigorously prove that the exponents of the BS model are the same above and below the transition. From our results it follows that all terms of the Taylor series of the scaling function $f(x)$ for the avalanche distribution are uniquely and explicitly determined by two critical exponents of the model. We expect that the usual restrictions on the shape of $f(x)$ indirectly relate these two exponents and, therefore, reduce the number of independent critical exponents in the BS model to just one.

As was described in [3], the avalanches in extremal models are defined from the value of the global minimal number $f_{\min}(s)$ as a function of time s . Then for any given value of the auxiliary parameter f_0 , an f_0 avalanche of size (temporal duration) S is defined as a sequence of $S - 1$ successive events with $f_{\min}(s) < f_0$ confined between two events with $f_{\min}(s) \geq f_0$, in other words, the time steps when $f_{\min}(s) \geq f_0$ divide the time axis into a series of avalanches, following one another. It is easy to see that an avalanche defined by this rule is nothing but a stochastic process in which numbers $f_i < f_0$ play the role of active particles that are randomly created or annihilated. The avalanche is terminated (and the next one is immediately started) when there are no particles left in the system. As in any other creation-annihilation processes (such as

directed percolation, for example) in the BS model there exists a critical value f_c of the creation probability f_0 , for which the creation of particles is marginally balanced by their annihilation, and avalanches of all sizes can be realized. In the stationary state of the BS model on the infinite lattice, $f_{\min}(s) \leq f_c$ for every s . Therefore, the overcritical ($f_0 > f_c$) region of the branching process parameters is not accessible, since there are no events starting or terminating such avalanches. However, if the system is artificially prepared in the overcritical state with $f_i \geq f_0 > f_c$ everywhere, one can observe overcritical avalanches. Another way to look into the overcritical properties of the model is to use the *BS branching process* [7] in the simulations of the model. In this process one only keeps track of the numbers $f_i < f_0$ and at each time step activates the smallest one of them. It was shown in [7] that the undercritical avalanches in the BS model are *exactly* equivalent to the realizations of the BS branching process. However, in the latter case, one can select $f_0 > f_c$ as well. Then there exists a nonzero probability $P_\infty(f_0)$ that the process will never stop (an infinite avalanche), but at the same time the size of finite avalanches acquires a finite cutoff.

We characterize an avalanche by two principal numbers: (1) S —the avalanche size, equal to its temporal duration; (2) n_{cov} —the number of sites covered (f_i was updated at least once) by the avalanche.

In one-dimensional models the connected nature of the set of covered sites ensures its compactness (absence of holes) and, therefore, n_{cov} is precisely equal to the avalanche spatial extent R . In higher dimensions (but below the upper critical dimension) it was conjectured in [3] that the set of covered sites is a nonfractal object of the same dimensionality d as the underlying lattice. This conjecture is based on the numerical observation that the mass dimension of the avalanche D , which relates the avalanche size S to its spatial extent R through

$$S \sim R^D, \quad (1)$$

is usually greater than the dimension of the “substrate” space d . Therefore, the set of covered sites, being the projection of all points in the avalanche along the temporal axis onto the substrate space, is likely to be a dense object, and the spatial size R of the avalanche can be *defined* by the relation $n_{\text{cov}} = R^d$.

The quantity of primary interest in the BS model is the probability distribution $P(S, f_0)$ of the avalanche sizes S at any given value of the auxiliary parameter f_0 . The moments in time, when $f_0 \leq f_{\min}(s) < f_0 + df_0$, serve as breaking points for f_0 avalanches but not for $f_0 + df_0$ avalanches. Therefore, when f_0 is raised by an infinitesimal amount df_0 some of f_0 avalanches *merge* together to form bigger ($f_0 + df_0$) avalanches. In the rest of this paper we study in more detail the properties of this merging process and the avalanche hierarchy that it induces.

The most important observation about f_0 avalanches in the BS model (as well as in several other extremal models, such as the Sneppen model [8] or invasion percolation [4]) made by Paczuski, Maslov, and Bak in [3,7] is that when an f_0 avalanche is terminated, the numbers f_i on the set of $n_{\text{cov}} = R^d$ updated sites are *uncorrelated and uniformly distributed between f_0 and 1*.

It was shown in [3,7] that the direct consequence of this observation is that the probability of an f_0 avalanche of spatial size R^d to merge with the subsequent one when the parameter f_0 is raised by df_0 is given by $R^d df_0 / (1 - f_0)$. (The merging occurs if at least one of the changed numbers falls in $[f_0, f_0 + df_0]$.) For the following arguments to be true it is important that any two subsequent avalanches are mutually uncorrelated. That is, the probability distribution of f_0 avalanches, starting immediately after the termination of an f_0 avalanche of a given size S , is independent of S . That is true for the BS model since the dynamics within an f_0 avalanche in the BS model is completely independent of the particular value of the numbers $f_i > f_0$ in the background that were left by the previous avalanches. This mutual independence may *not be the case* for other extremal models such as the Sneppen model or invasion percolation.

Now we are in a position to write the *exact* master equation describing how the avalanche merging changes $P(S, f_0)$ as f_0 is raised. Let $R^d(S, f_0)$ be the average number of updated (covered) sites in an f_0 avalanche of temporal size S . From our simulations of the BS model [3] we know that, for f_0 close to f_c , $R^d(S, f_0)$ scales with S as $S^{d/D}$ [see Eq. (1)]. However, for the following arguments any form of $R^d(S, f_0)$ will suffice. The master equation for $P(S, f_0)$ can be written as

$$(1 - f_0) \frac{\partial P(S, f_0)}{\partial f_0} = - P(S, f_0) R^d(S, f_0) + \sum_{S_1=1}^{S-1} P(S_1, f_0) R^d(S_1, f_0) \times P(S - S_1, f_0). \quad (2)$$

Here the first term describes the loss of avalanches of size S due to the merging with the subsequent one, while the second term describes the gain in $P(S, f_0)$ due to the merging of avalanches of size S_1 with avalanches of size $S - S_1$. Unlike in a conventional master equation, the parameter f_0 in our master equation is not time. It is convenient to change variables from f_0 to $g = -\ln(1 - f_0)$, so that $f_0 = 0$ corresponds to $g = 0$, $f_0 = 1$ corresponds to $g = +\infty$, and $dg = df_0 / (1 - f_0)$. This change is due to the fact that, although traditionally new random numbers are drawn from the flat distribution $\mathcal{P}(f_0) = 1$, the “natural” distribution for the BS model has the probability density $\mathcal{P}(g) = e^{-g}$. As usual, the critical properties of the model are independent of the particular shape of \mathcal{P} . In the rest of the paper we will use the natural variable g instead of f_0 .

Equation (2) can be conveniently written in terms of Laplace transforms $p(\alpha, g) = \sum_{S=1}^{\infty} P(S, g)e^{-\alpha S}$ and $r(\alpha, g) = \sum_{S=1}^{\infty} P(S, g)R^d(S, g)e^{-\alpha S}$ as $\partial p(\alpha, g)/\partial g = -r(\alpha, g) + p(\alpha, g)r(\alpha, g)$, or simply

$$\partial \ln[1 - p(\alpha, g)]/\partial g = r(\alpha, g). \quad (3)$$

This exact equation is the central result of this paper. It has many interesting physical consequences. When $g < g_c$ all avalanches are finite ($P_{\infty} = 0$) and normalization requires $p(0, g) = \sum_{S=1}^{\infty} P(S, g) = 1$. From the general properties of the Laplace transform one can write the Taylor series for $p(\alpha, g)$ and $r(\alpha, g)$ at $\alpha = 0$ as $p(\alpha, g) = 1 - \langle S \rangle_g \alpha + \langle S^2 \rangle_g \alpha^2/2 - \langle S^3 \rangle_g \alpha^3/6 + \dots$ and $r(\alpha, g) = \langle R^d \rangle_g - \langle R^d S \rangle_g \alpha + \langle R^d S^2 \rangle_g \alpha^2/2 - \dots$. Substitution of these expressions into Eq. (3) results in $\partial/\partial g \ln(\langle S \rangle_g \alpha - \langle S^2 \rangle_g \alpha^2/2 + \dots) = \langle R^d \rangle_g - \langle R^d S \rangle_g \alpha + \langle R^d S^2 \rangle_g \alpha^2/2 + \dots$. Since Eq. (3) holds for arbitrary α , comparing the coefficients of different powers of α in the above Taylor series results in an infinite series of exact equations. Comparison of the coefficients of α^0 gives

$$d \ln \langle S \rangle_g / dg = \langle R^d \rangle_g. \quad (4)$$

This is exactly the ‘‘gamma’’ equation derived in [9].

Higher powers of α in Eq. (3) give new exact equations. Here we show just the first two:

$$\frac{d}{dg} \left(\frac{\langle S^2 \rangle_g}{\langle S \rangle_g} \right) = 2 \langle R^d S \rangle_g, \quad (5)$$

$$\frac{d}{dg} \left(\frac{\langle S^3 \rangle_g}{3 \langle S \rangle_g} - \frac{\langle S^2 \rangle_g^2}{2 \langle S \rangle_g^2} \right) = \langle R^d S^2 \rangle_g. \quad (6)$$

The Taylor expansion changes slightly in the overcritical region, where there is a finite probability $P_{\infty}(g)$ to start an infinite avalanche. Since the avalanche distribution $P(S, g)$ is limited to finite avalanches, it is naturally normalized to $1 - P_{\infty}(g)$. Therefore, when $g > g_c$ the Fourier series for $p(\alpha, g)$ can be written as $p(\alpha, g) = 1 - P_{\infty}(g) - \langle S \rangle_g \alpha + \langle S^2 \rangle_g \alpha^2/2 + \dots$. Now the comparison of the coefficients at α^0 in Eq. (3) gives

$$d \ln P_{\infty}(g) / dg = \langle R^d \rangle_g. \quad (7)$$

This new equation is the $g > g_c$ analog of the gamma equation (4). We will refer to it as ‘‘beta’’ equation [the exponent β is traditionally used for the scaling of $P_{\infty}(g)$, while $-\gamma$ is used for $\langle S \rangle_g$].

There is a more straightforward way to derive Eq. (7) from the average properties of the merging process. The merging of finite and infinite avalanches gives an infinite avalanche and, therefore, leads to an increase in $P_{\infty}(g)$. The average probability of finite avalanche merging with the next one as g is increased by dg is $\langle R^d \rangle_g dg$, and the probability that this next avalanche happens to be an infinite one is $P_{\infty}(g)$. Therefore, $dP_{\infty}(g) = P_{\infty}(g) \langle R^d \rangle_g dg$, which is just Eq. (7).

As in the undercritical case, the Taylor expansion of Eq. (3) for $g > g_c$ determines an infinite series of exact

equations. The first two of them are

$$\frac{d}{dg} \left(\frac{\langle S \rangle_g}{P_{\infty}(g)} \right) = -\langle R^d S \rangle_g, \quad (8)$$

$$\frac{d}{dg} \left(\frac{\langle S^2 \rangle_g}{P_{\infty}(g)} + \frac{2 \langle S \rangle_g^2}{P_{\infty}(g)^2} \right) = -\langle R^d S^2 \rangle_g. \quad (9)$$

As in other creation-annihilation branching processes, the avalanche distribution $P(S, g)$ in the BS model for $g < g_c$ is known to have a scaling form

$$P(S, g) = S^{-\tau} f(S^{\sigma}(g - g_c)), \quad (10)$$

where τ and σ are some critical exponents and $f(x)$ is a scaling function that rapidly decays to zero as $x \rightarrow -\infty$. From (10) it follows that the average avalanche size diverges when g approaches g_c from below as $\langle S \rangle_g \sim (g_c - g)^{-\gamma}$, where $\gamma = (2 - \tau)/\sigma$. Substitution of this expression into the gamma equation (4) results in

$$\langle R^d \rangle_g = \gamma / (g_c - g), \quad \text{for } g < g_c. \quad (11)$$

The exponent relation derived from (11) connects σ to D and τ : $\sigma = 1 + d/D - \tau$ [3]. It is easy to see that Eqs. (5)–(9) do not yield additional exponent relations but further restrict the exact form of the avalanche distribution scaling function $f(x)$.

The scaling should work in the overcritical regime as well. However, unlike in the equilibrium statistical mechanics, the critical exponent σ can *a priori* be different above and below the transition. In what follows we show that, at least for the BS model, this is not true. Substitution of the scaling form $P_{\infty}(g) \sim (g - g_c)^{\beta}$ into the beta equation (7) results in

$$\langle R^d \rangle_g = \beta / (g - g_c), \quad \text{for } g > g_c. \quad (12)$$

From (12) it follows that the same exponent relation $\sigma = 1 + d/D - \tau$ holds in the overcritical region, and, therefore, the exponent σ is the same above and below the transition. The scaling form (10) can now be extended to include the overcritical region $S^{\sigma}(g - g_c) > 0$. As in various percolation problems [10] the scaling form (10) for $P(S, g)$ at $g > g_c$ results in the exponent relation $\beta = (\tau - 1)/\sigma$. An interesting consequence of exact Eqs. (11) and (12) is that the universal amplitude ratio for $\langle R^d \rangle_g$ is given by the ratio of two critical exponents

$$\frac{\langle R^d \rangle_{g+\Delta g}}{\langle R^d \rangle_{g-\Delta g}} = \frac{\beta}{\gamma} = \frac{\tau - 1}{2 - \tau}. \quad (13)$$

This unusual relation between the universal amplitude ratio and critical exponents is, to our knowledge, unique for the BS model.

There is a case when the master equation (3) can be written in a closed form. This is the extensively studied [11,12] mean field random neighbor version of the BS model, where, at each time step $K - 1$, ‘‘neighbors’’ of the active site are selected in an annealed random fashion throughout the whole system. It is easy to see that in

the thermodynamic limit of this model the number of updated sites in the avalanche of temporal duration S is given by $n_{\text{cov}} = (K - 1)S + 1$. This is the quantity that should be used instead of $R^d(S, g)$ in our equations. The missing equation connecting $r(\alpha, g)$ and $p(\alpha, g)$ is $r(\alpha, g) = -(K - 1)\partial p(\alpha, g)/\partial \alpha + p(\alpha, g)$, and the final form of Eq. (3) for the mean field BS model is

$$\frac{\partial \ln[1 - p(\alpha, g)]}{\partial g} = -(K - 1)\frac{\partial p(\alpha, g)}{\partial \alpha} + p(\alpha, g). \quad (14)$$

This equation should be solved with the initial condition $p(\alpha, 0) = e^{-\alpha}$, since $P(S, 0) = \delta_{S,1}$. We checked that for $K = 2$ the generating function

$$\begin{aligned} \sum_{S=1}^{\infty} P(S, f_0)x^S \\ = \frac{1 - 2xf_0(1 - f_0) - [1 - 4xf_0(1 - f_0)]^{1/2}}{2f_0^2x}, \end{aligned}$$

derived in [12] using different methods, after the substitution of $x = e^{-\alpha}$ and $f_0 = 1 - e^{-g}$ satisfies (14) and has the correct initial condition. That confirms the overall consistency of our approach.

It can be shown [13] that for any given τ and σ , the Eq. (3) recursively defines all terms in the Taylor series of the scaling function $f(x)$ at $x = 0$:

$$\begin{aligned} f^{(n+1)}(0) &= \sum_{n_1+n_2=n} \frac{\Gamma(1 - \tau + \sigma n_1)\Gamma(\sigma + \sigma n_2)}{\Gamma(1 - \tau + \sigma + \sigma n)} \\ &\times \frac{n!}{n_1! n_2!} f^{(n_1)}(0)f^{(n_2)}(0), \end{aligned}$$

where $\Gamma(x)$ is the Euler's gamma function. We suspect that for any given d/D there exist unique τ and $\sigma = 1 + d/D - \tau$ such that the scaling function satisfies all usual requirements, such as $f(x) \rightarrow 0$, when $x \rightarrow \pm\infty$, and $\int_0^\infty x^{-\tau}[f(0) - f(-x^{1/\nu})]dx = 0$ (the absence of the infinite avalanche below g_c). Which of these constraints indirectly defines τ as a function of d/D remains to be determined. The numerical solution of Eq. (2) with $R^d(S, f_0) = AS^{d/D}$ indeed seems to give the correct value for τ [13]. In Fig. 1 we present the results of the numerical solution of Eq. (2) with $R^d(S, f_0) = S^{0.412}$, corresponding to the best numerical estimate of d/D in the one-dimensional BS model [3,14]. The solution indeed yields $\tau = 1.1 \pm 0.1$ which is consistent with $\tau = 1.07 \pm .01$ determined by extensive Monte Carlo simulations [3,14].

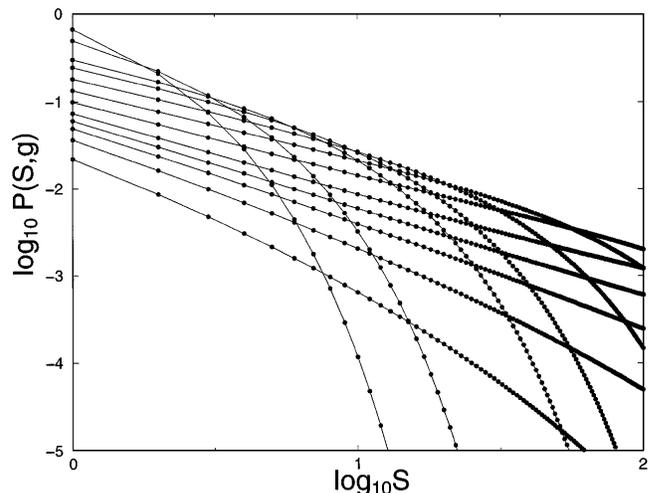


FIG. 1. The results of the numerical solution of Eq. (1) on the interval $1 \leq S \leq 100$ with $R^d(S, g) = S^{0.412}$. Values of g increase from top to bottom. The exponent of the power law part was measured to be 1.1 ± 0.1 .

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